HERMAPHRODITIC FLOWERS IN CALIFORNIAN OAKS

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In late summer 1941, a shrub of *Quercus turbinella* Greene subsp. *californica* Tucker was noticed flowering out of season beside U.S. Highway 399 at the base of the north side of Pine Mountain, Ventura County. Here, at an elevation of 3900 feet, this small-leaved, sclerophyllous oak occurred in an open, xeric shrub association with *Ceanothus leucodermis* Greene and *Pinus monophylla* Torr. & Frem. Although this oak is common in the area, only the one shrub was observed to be flowering.

The inflorescences, arising from buds at the ends of the twigs or in the upper leaf axils, were much longer than normal—up to 5 cm in length (fig. 1,A). The stiff rachis commonly was more slender distally, and sometimes had a slightly zigzag course. In some spikes the several lower flowers were perfect and the rest staminate. In addition to these aberrant inflorescences, the shrub also bore many clusters of apparently normal staminate aments. In the aberrant inflorescences, the individual flowers were bracteate, up to 3.5 mm in length, and had the appearance of pistillate flowers (as, indeed, some of them were: fig. 1,C) with stamens added. The stamens were in an epigynous position (see fig. 1,B), centripetal to the very small perianth lobes.

All species of *Quercus* are normally monoecious. In *Q. turbinella* subsp. *californica,* the pistillate flowers occur one or two together, usually sessile in the axils of the upper leaves of the new shoots. The staminate flowers, which appear in much greater numbers, are in lax, elongated catkins borne on the lower portion of the newly elongating leafy shoot or emerging from buds clustered at the ends of the previous year's twigs.

In the present case, both the flowers and the time of flowering were unusual. My observations (and collection: *Tucker 373-A,* DAV) were made on August 9, 1941; however, in that general area, *Q. turbinella* subsp. *californica* normally flowers in April. Although no unusual environmental conditions were noted at the time, this unusual flowering must have been triggered by some sort of unusual conditions (and the *initiation* and early differentiation of these inflorescences and flowers must have occurred at least several weeks prior to that).

Again, in late summer 1947, the same type of peculiar flowering was noted on a shrub of *Q. durata* Jeps. in Marin County, beside the Fairfax-Alpine Dam road, opposite the south end of Carson Ridge (*Tucker 1588,* August 31, 1947. DAV). This oak, like *Q. turbinella,* is a drought-adapted, small-leaved, sclerophyllous shrub. The stiff, elongated, multi-flowered spikes bore mostly pistillate flowers, but a few of the flowers had small epigynous stamens, also. At this latitude, *Q. durata* normally flowers in May.

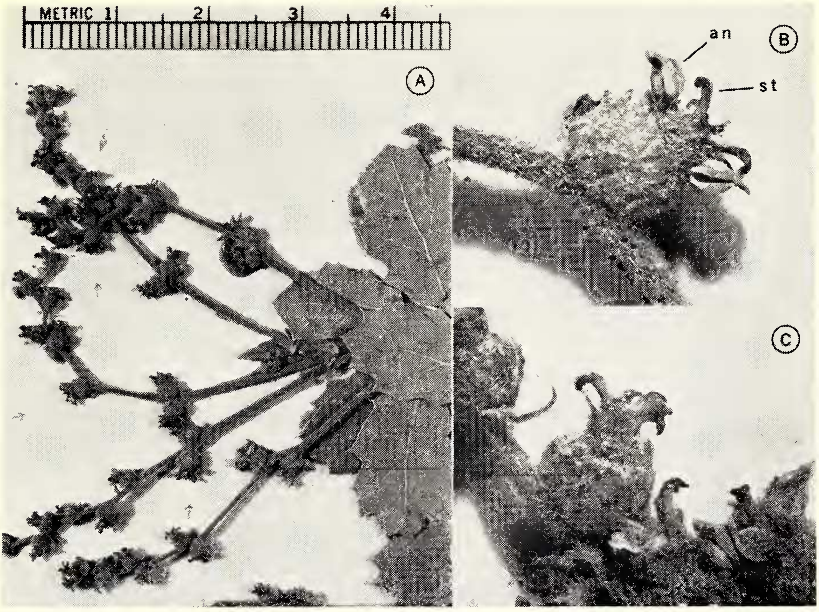

FIG. 1. Inflorescences and flowers of *Quercus turbinella* subsp. *californica:* A. Atypical inflorescences bearing mostly perfect flowers; B, An individual perfect flower; C, A pistillate flower (center) in an inflorescence composed largely of perfect flowers. (an: anther; st: style)

In the genus *Quercus,* instances of this sort may be quite rare, but probably not so rare as the paucity of published reports might indicate. Scaramuzzi (1958) reported similar atypical flowers in the Mediterranean oak, *Q. coccifera* L. She encountered this in mid-May rather than late summer, however, and noticed no disruptive agents in the external environment. In addition to hermaphroditic flowers, she also described two types of intersexual flowers in which either the stamens or the pistils were more strongly developed. I am aware of only one previously published account of unseasonal perfect flowers in the United States. Greene (1889–90) reported exactly this condition in *Q. agrifolia* Née and *Q. dumosa* Nutt., both from Santa Cruz Island, off the coast of southern California. Although he illustrated this condition of *Q. dumosa* (op. cit., Plate XXVIII), his figure is only a gross depiction of the inflorescences—the hermaphroditic nature of the flowers is not shown at all. It seems worthwhile, therefore, to put on record these instances I have observed and illustrations showing the actual flowers.

There is considerable evidence that the perfect flower represents the ancestral condition in the Fagaceae (Reece, 1938; Tucker, unpubl.), and that typical unisexual flowers represent a derived condition attained through evolutionary reduction—presumably by the accumulation of gene mutations over a period of time—that ultimately suppressed initiation of the stamens in certain flowers (the pistillate flowers) and initiation of the gynoecium in others (the staminate flowers). But gene action is always expressed against a background of environmental conditions and, considering the readiness with which the "normal" sexual expression of certain flowers can be altered experimentally (e.g., *Cannabis*, Heslop-Harrison, 1959; *Cucurbita*, Nitsch et al., 1952), one can easily visualize similar effects being produced in nature by the infrequent occurrences of unusual environmental conditions. In other words, if an oak (which normally produces only unisexual flowers) were subjected to environmental conditions that differ markedly from the norm at the period of floral initiation and early development, this "latent" potential to produce hermaphroditic flowers might still be realized.

The external factors in the natural environment of foremost importance in floral initiation are usually temperature and light (Hillman, 1962). Any drastic deviation from the norm of mature floral organization (as in the present case) probably reflects some unusual condition in one or both of these factors during floral initiation and early development. However, the presence of normal staminate aments in the same flush of unseasonal growth—indeed, on the same branchlet—indicates that the unusual condition(s) must have affected only the pistillate spikes, producing three gross visible aberrations: (1) a much more elongated axis, (2) many more flowers than normal, and (3) the presence of stamens in some of them (i.e., altering them from pistillate to hermaphroditic).

In the oaks, flowers on the spring flush of growth are initiated the previous year. Thus, in *Q. alba*, Turkel et al. (1955) observed that both staminate and pistillate inflorescences are initiated during the year preceding anthesis, the staminate inflorescences being distinguishable as early as late June. Similarly, Conrad (1900) observed that in winter buds of *Q. velutina* the staminate flowers already had stamens well formed, and the carpels were evident in the pistillate flowers.

The aberrant inflorescences with which we are concerned, however, represent new flushes of growth in late summer, borne on the twigs formed that same spring. The conditions that induced the formation of these atypical inflorescences and flowers must have been operative only two or three months prior to these unseasonal August flowerings.

In my field notes for the *Q. durata* collection, this comment appears: "The unusual out-of-season aments may be correlated with the unseasonal rains of May and June of this year." A check of U.S. weather Bureau records (1941, 1947, 1964) indicates that there was, indeed, unusual precipitation in late spring and/or summer both in 1941 in Ventura County and in 1947 in Marin County. Ozena, in the upper Cuyama Valley in Ventura County—a weather station since 1906—is within a mile of the location of the *Q. turbinella* collection. Kentfield, in Marin County—a weather station since 1888, and the nearest one to the collection site of *Q. durata*—is roughly seven miles (airline) east of the *Q. durata* locality.

Strangely enough, the seasonal precipitation records for these two years and localities were quite different. At the Ozena station, 1941 was an unusually wet year; at the Kentfield station, 1947 was comparatively a very dry year. A major point of similarity, however, may be noted. At Ozena, May was significantly wetter than normal in 1941. Similarly, at Kentfield, June was notably wetter than normal in 1947. These atypically late rains, *after the oaks put out their normal spring flush of growth,* may possibly have triggered this second flush of growth. On the other hand, the initiation and early development of these flowers most likely was the result of some other combination of factors (probably temperature and day length, and perhaps others). Temperature data for 1941 was not available for the Ozena station. Data for Kentfield for 1947, however, indicate temperatures slightly higher than normal during the several months preceding the aberrant flowering of *Q. durata* in August. The monthly mean temperatures for May, June, and July were respectively, 3.4, 3.1, and 1.7 °F above the long term mean monthly temperatures (based on a 51-year record).

Considering these aberrant inflorescences, once again, their most obviously deviant features are (1) their much greater length, and (2) more numerous flowers. Some insight as to the underlying causes may be gained from the study by Turkel et al. (1955), who noted that in the early development of the pistillate inflorescence in *Q. alba* a number of bractlets appear in rapid succession along the primordial inflorescence axis. A flower develops in the axil of each of the lower bractlets, and these flowers become the (one to several) functional pistillate flowers. In addition, however, rudimentary flowers in various stages of development occur at the apex of the axis. Macroscopically, this tip of the axis, with its bractlets and rudimentary flowers, appears merely as a slight continuation above the functional flowers. Also, in *Q. borealis* Michx. f. (*Q. rubra* L.), a member of the black oak subgenus, the primordial pistillate inflorescence contains a number of bracts arranged spirally on the axis, but floral apices form in the axils of only the two (or occasionally one) lowest bracts (Macdonald, 1971).

It seems likely that this early suppression of some of the pistillate flowers is a fairly general feature in *Quercus,* most species of which have short, few-flowered pistillate inflorescences at anthesis. This view gains credence, furthermore, when we consider the fact that a few Mexican and Central American species are *characterized* by elongated, multiflowered pistillate inflorescences (e.g., *Q. rugosa* Née among the white oaks, and *Q. urbanii* Trel. among the black oaks). In the related but generally more primitive genus *Lithocarpus,* elongated, many-flowered inflorescences are common (see Camus, 1948). These facts suggest that in species such as *Q. alba,* or *Q. borealis,* the production of only one or two mature pistillate flowers—when the *potential* for more development is clearly present—may be the result of growth hormones that suppress this development. If, then, the "normal" auxin regime were upset on rare occasions by a marked change in environmental conditions, perhaps this potential would be realized and ancestral gene combinations still in the code, but long suppressed, would be re-activated to produce not only elongated, multi-flowered inflorescences but hermaphroditic flowers as well. Even so, it appears that it is only the rare individual that is capable of this kind of response, for this aberrant flowering has been observed only in single individuals—not throughout populations. However, fundamental answers to such questions of cause and effect must await further study, and as a subject for experimental morphogenesis this one would be interesting indeed.

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NOTES AND NEWS

CYTISUS SCOPARIUS (L.) LINK IN NORTH CENTRAL IDAHO.—*Cytisus scoparius* (L.) Link is a very common adventive, that is well established and spreading rapidly in many places on the w. side of the Cascades, from Calif. to B.C. (Hitchcock, et al. 1961. Vascular Plants of the PNW.; Vol. 3). While the shrub is sometimes cultivated east of the Cascades, previous to this report, it was not known as an escape from there. Several large bushes of Scots broom were observed growing in the wild along the St. Joe River road near the Falls Ck. bridge, Shoshone Co., Idaho (*Layser and Phillips 1441*, WS).—EARLE F. LAYSER, Colville Natl. Forest, Colville, Washington 99114 and H. WAYNE PHILLIPS, Helena Natl. Forest, Helena, Montana 59601.